SCLEROCHRONOLOGY AND CARBONATE PRODUCTION IN SOME UPPER JURASSIC REEF CORALS

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ABSTRACT. Annual banding evident from epithecal increments and associated internal structural changes in phaceloid and massive Oxfordian corals show a range in growth rate from 5 to 10 mm yr^{-1} in branching colonies (*Thecosmilia*) and 1.5 to 3 mm yr^{-1} for massive colonies (*Thamnasteria*, *Fungiastraea*, *Isastraea*). High- and low-density growth bands are identified in massive colonies. The denser part of each couplet is consistently the broader, in contrast with that of most shallow-water modern corals. This is interpreted as due to high local turbidity. The formation time for two sections is estimated with gross carbonate production of 2000 to 3300 g CaCO$_3$ m^2 yr^{-1}.

GROWTH bands in organisms are of great interest to biologists and palaeontologists because, where their periodicity can be determined, a means is provided to estimate growth rate and age. Although growth bands have been studied in several groups of marine invertebrates most interest has been shown in scleractinian reef-building corals because of the extensive distribution of modern corals and ancient coralliferous sediments. Hudson *et al.* (1976) have coined the term sclerochronology to describe coral growth band studies, in comparison with the well-known term dendrochronology (e.g. Jefferson 1982). Research has been mainly concerned with the nature of the growth banding, its ecological significance and applications in the biological (Buddemeier and Kinzie 1976) and geophysical sciences (Rosenberg and Runcorn 1975; Scrutton 1978).

No growth studies have hitherto been made of Mesozoic corals but several British upper Jurassic corals display banding on well-preserved epithecae or in longitudinal section. The purpose of the present study is to examine the nature and periodicity of growth bands in the common branching and massive corals from the Oxfordian of England, and to assess their environmental implications, the time represented by particular coralliferous units, and the rate of carbonate production. Less-common genera such as *Rhabdophyllia* and *Montlivaltia*, which are seldom well preserved, and several genera recorded only from Steeple Ashton (Negus and Beauvais 1979) are not considered in any detail. Other invertebrates associated with coralliferous units, such as oysters, species of *Chlamys*, *Lithophaga*, and the alga *Solenopora* also show growth bands suggestive of annual periodicity but details are not included here.

Although there are many papers concerned with special aspects of the Oxfordian rocks of England, Arkell (1933, 1947) provides accounts of the distribution and stratigraphy of the outcrops and Cope *et al.* (1980) provides correlations. Material on which this paper is based was collected in the course of an investigation of coralliferous units in the Corallian (Oxfordian) of England (Ali, unpublished Ph.D. thesis, University of Reading, 1978) from the following: Shellingford Cross-Roads Quarry (SU 327941) (Arkell 1947, p. 87), Kingsdown Farm (temporary section) (SU 175885), Cumnor Hill by-pass (temporary section) (SP 465040) (see Arkell 1947, p. 89), Headington Cross-Roads Quarry (SP 550064) (Arkell 1947, p. 94), Steeple Ashton (ST 9057) (Negus and Beauvais, 1979); Yorkshire (Wright 1972), Ayton Quarry (TA 002856), Crossgate Quarry, Seamer (TA 028843), Pockley Quarry (SE 635846), Nunnington railway cutting (SE 649787), Stonegrave Quarry (SE 648787).
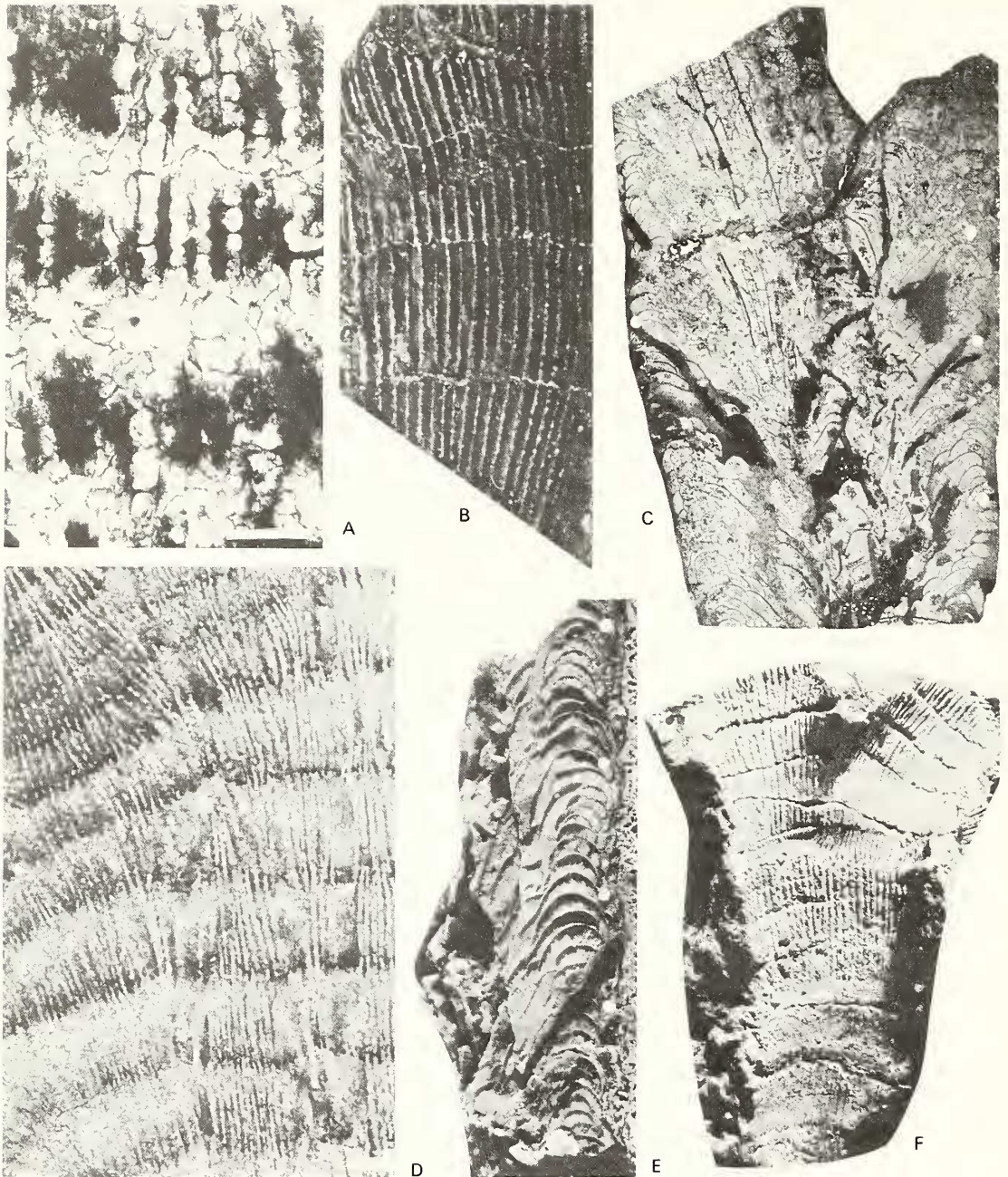
TEXT-FIG. 1. *Fungiastrea arachnoides*. A, photomicrograph of unstained thin-section with neomorphic preservation, showing banding and a few more complete upward-tapering septa, ×25. D, positive print from stained longitudinal thin-section showing dark zones with thick septa and light zones with poor preservation of skeletal elements, ×6. Shellingford Cross-Roads Quarry (Reading University 14876a, b). B, C, E, F, *Thecosmilia annularis*. B, latex peel from external mould of partly decorticated specimen, ×2. C, longitudinal section with tabular dissepiments marked (for comparison with text-fig. 3B), ×1.5. Shellingford Cross-Roads Quarry (RU 14879). E, periodic development of tabular (marked) and vesicular dissepiments, ×2. Cumnor By-pass. F, external mould of partly decorticated specimen showing major concentric markings associated with abrupt thickening of septa, ×1.2. Shellingford Cross-Roads Quarry (RU 14877). Bar scales: A, 0.5 mm; D, 1.0 mm.

GROWTH BANDS

MASSIVE CORALS

Thamnasteria concinna (Goldfuss), *Fungiastraea arachnoides* (Parkinson), and *Isastraea explanata* (Goldfuss).

The three species of massive corals show distinct banding on longitudinal sections and on differentially weathered material, mostly as an alternation of a broader dark zone with thicker septa and a narrower zone with less distinct and thinner skeletal elements (text-fig. 1A, D).

The two zones are similar to bands recognized in modern scleractinian reef corals by several authors (e.g. Knutson *et al.* 1972) and referred to as high- and low-density bands. Using x-radiographic techniques Knutson *et al.* (1972), Buddemeier (1974), Buddemeier *et al.* (1974), MacIntyre and Smith (1974), Dodge *et al.* (1974), Dodge and Thomson (1974), and Weber *et al.* (1975) showed that a high- and low-density couplet is deposited yearly by many tropical corals.

In the Oxfordian material the couplets have been diagenetically enhanced so that they are visually distinct. Both zones have undergone neomorphic replacement by calcite or ferroan calcite, but the skeletal relics are best preserved in the lower darker zone and relatively uncommon in the lighter zone (text-fig. 1A). Ferroan calcite is mainly in the upper zone. In thin section the change from one zone to another is generally sharp and distinct due to the contrasting degree of recrystallization. The differential recrystallization may be related to primary skeletal thickness and composition and to differences in the original skeletal porosity. An attempt was made to determine whether any variation in non-carbonate (clay) inclusions now occurs between the couplet zones. Selected specimens showing clear banding were analysed for Si, Ca, and Fe using electron probe. The results (in Ali unpublished Ph.D. thesis, University of Reading, 1978) show that there is no clear correlation between the slight variations in these constituents and position of individual bands.

Couplet widths were measured on sectioned specimens and peels where preservation of the skeletal elements was deemed satisfactory. Poor relic preservation often overemphasizes the light zone when it may be questioned which zone is equivalent to the high- and low-density band of modern corals. The light zone was also prone to recrystallization with void stage. Dr. D. Kinsey (Australian Institute of Marine Science, Townsville) suggested to Dr. R. Goldring that the low-density band with its inferred greater amount of organic matter (Highsmith 1979) might fossilize relatively better than the high-density band, but this does not seem to have been the case. No significant variation in width of the high- and low-density bands has been noted between the bottom and top of colonies investigated, although there is an irregular variation through and laterally across a colony. The zones are occasionally of equal width but the ratio of the width of the light zone to that of the dark zone is never greater than 1·0 (text-fig. 2). This contrasts with modern shallow-water reef genera where it is the dense band that is
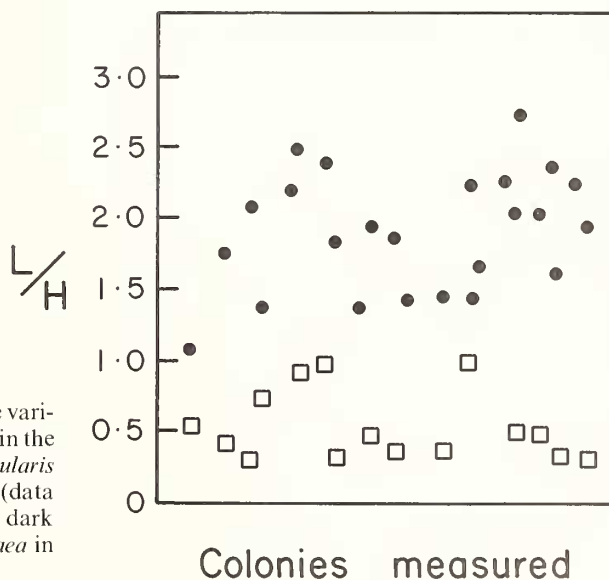
TEXT-FIG. 2. Graphical representation to illustrate variation in ratio (L/H) of low- to high-density bands in the modern corals *Platygyra* sp. and *Montastrea annularis* from Indo-Pacific and Caribbean localities ● (data from Weber *et al.* 1975) and the ratio of light to dark zones in *Thamnasteria*, *Fungiastraea*, and *Isastraea* in the Oxfordian of England □.

thinner (e.g. Knutson *et al*. 1972; MacIntyre and Smith 1974; Baker and Weber 1975; Weber *et al*. 1975). Weber *et al*. (1975) show that the ratio low density/high density is always greater than 1·0 and up to 2·8. But Highsmith (1979) and Hudson (1981) find ratios of less than 1·0 associated with growth in deeper water.
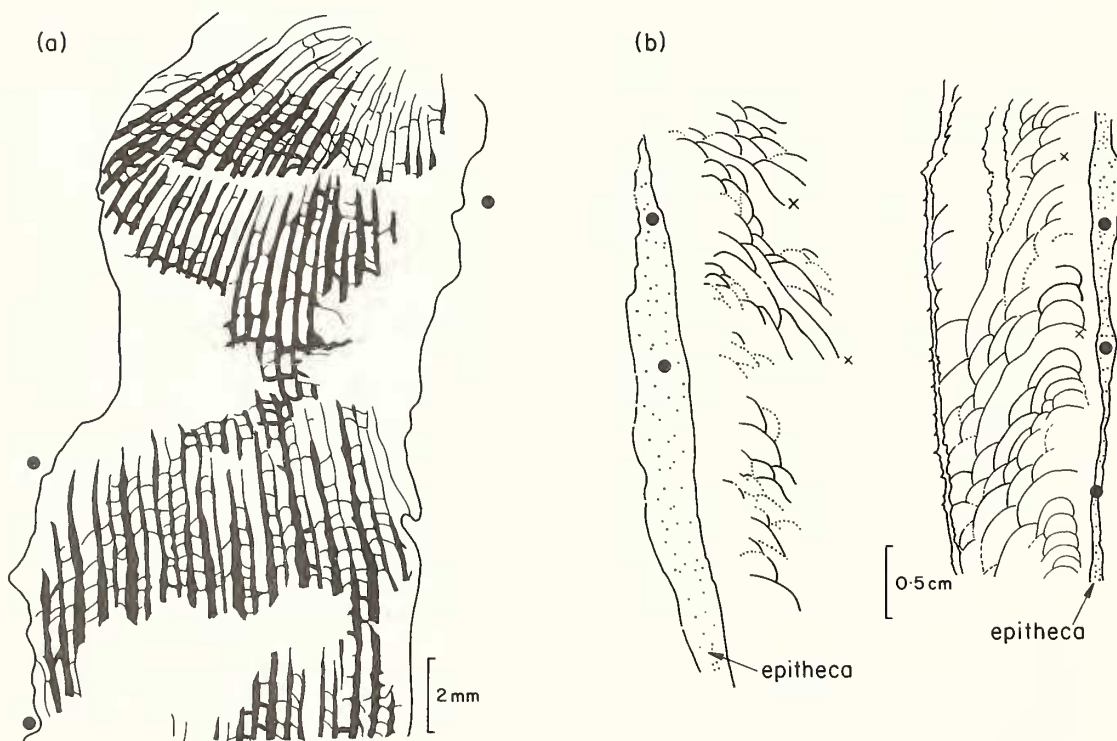
Thecosmilia annularis (Fleming).

T. annularis is a common phaceloid coral in most sections. Incremental growth is evident on the epitheca and there are related structural changes to septa and dissepiments.

(*a*) *Epithecal banding*. Where the epitheca is well preserved, or on good external moulds a regular banding of major concentric markings separated by areas with finer incremental ridges may be seen. Whilst the major growth bands (4 to 6 in 50 mm) are well defined and easy to follow, the fine bands (more than 200 in 10 mm) are generally indistinct and very difficult to trace on the material available. It has not been possible to establish the number of fine bands between major growth bands.

(*b*) *Structural changes*. The major banding (above) is expressed internally by a sharp thickening of the septa (text-fig. 1B, F) which gradually thin upwards to the next thickening. This is best seen on partly decorticated specimens preserved as external moulds. The arrangement of tabular vesicular dissepiments shows a close relationship to the major growth banding (text-figs. 1C, E, 3). Following formation of a tabular dissepiment, the marginal vesicular dissepiments show a regular change mostly realized by transverse contraction towards the

TEXT-FIG. 3. *Thecosmilia annularis. a*, longitudinal section to show regular thickening and thinning of septa, *b*, longitudinal sections to show structural changes in dissepiments. ● Position of major epithecal banding, × tabular dissepiments (Reading University, 14878).

margin, abaxially. At the same time successively shorter dissepiments are introduced axially which maintain the general form of the calyx. Nevertheless, the introduction of a tabular dissepiment, which reached to about four-fifths the transverse length of a septum, led to a deepening and increased acuity of the thecal cone. The vesicular dissepiments are frequently thickened and crowded below the periodically introduced tabular dissepiment. This cyclicity or succession of dissepiment arrangement is rarely perfect, but the spacing of the tabular dissepiments corresponds with that of the major growth bands of the epitheca.

No such structural changes have yet been described in modern phaceloid corals but the general changes in thickness of septa and dissepiments are similar to those observed in modern massive corals and the Oxfordian genera. Ma (1934) described similar changes in the vesicular elements of modern and subfossil plocoid *Favia speciosa* though MacIntyre and Smith (1974) commented that dissepiment spacing does not differ between high- and low-density bands of *Pavona gigantea*. It seems reasonable to suppose that the periodic changes in *Thecosmilia* do represent annual changes and that the fine incremental ridges on the epitheca represent daily growth increments.

DISCUSSION

There can now be no doubt that each couplet of growth bands in modern corals represents an annual skeletal increment (Knutson *et al.* 1972; MacIntyre and Smith 1974; Moore and Krishnaswami 1974; Dodge and Thomson 1974; Weber *et al.* 1975). But what is not yet clear, as Scrutton (1978) and Scrutton and Powell (1980) discuss, are the environmental factors that contribute to the formation and seasonal timing of bands of different densities. (There is also as yet no detailed geochemical analysis of the differences between the different density bands and it would be premature to analyse, e.g. O_2 isotope, the banding of fossil corals.) Attempts to determine growth factors have, so far, led to somewhat contradictory conclusions. Some investigators (Dodge and Thomson 1974; Knutson and Buddemeier 1973; Buddemeier *et al.* 1974) suggest that high density is associated with seasonal low water temperature, whereas others (MacIntyre and Smith 1974; Weber and White 1974; Weber *et al.* 1975; Hudson *et al.* 1976; Isdale 1977) report that high skeletal density is correlated with periods of high water temperature. Buddemeier (1974) has correlated the dense bands with times of high seasonal rainfall and hence lower-light intensity. Stearn *et al.* (1977), using seasonal variations in the Barbados environment, suggest that the high-density bands are formed in the autumn in response to relatively abrupt decreases in the available light and the low-density bands are formed in the spring and summer.

The paired zones in Oxfordian corals must represent periods of significantly different conditions of skeletal gowth but it is difficult to draw from the fossil record what environmental factors led to the formation of different densities. England during the upper Jurassic was at about 40° N. (Smith *et al.* 1981) and a marked seasonality of climate is likely. If the negative correlation between skeletal density in corals and available light is accepted, then several characteristics of the corals may be explained.

The contrast in thickness ratios of low- to high-density growth between the Oxfordian corals and *Platygyra* and *Montastrea* (Weber *et al.* 1975) might be explained by presuming generally reduced light conditions in the local ancient seas because of either greater water depth or turbidity (see Highsmith 1979 for discussion). This would have allowed growth of a wider band of high-skeletal density and a much thinner band of low-skeletal density. In *Montastrea* (Baker and Weber 1975) the relative thickness of the band changes with depth. Whilst at depths of less than 18·0 m the less-dense band is consistently more than twice the width of the denser band, at greater depths this value changes to less than 0·5 coinciding with a sharp change in linear growth rate, skeletal density, and growth form. However, the actual thickness of the denser band shows relatively little change with depth. Hudson (1981) reported decrease in growth-rate of *Montastrea* in deeper fore-reef locations. The local reduced light intensity may better be attributed to high turbidity in the Corallian reefs (Ali, in preparation). Evidence in support of this is the absence of calcareous algae and foraminiferal encrusters, except for rare occurrences on massive corals. Although detritus trapped within the coral skeleton is widespread (e.g. Ali 1983), it is not possible to prove that in any instance it was introduced during growth as described by Bernard *et al.* (1974).

GROWTH RATES

In reviewing growth rates of modern scleractinian corals Buddemeier and Kinzie (1976) conclude that linear growth-rate ranges from 4 to 20 mm yr^{-1} and that normal average growth rate is about 10–12 mm yr^{-1}. They mention examples of faster growth and the extreme growth rate exhibited by *Acropora*. Dodge and Vaisnys (1977) give a vertical growth rate of about 3·5 mm yr^{-1} for Bermuda corals. Such gowth rates for modern corals may be used as a background for the study of growth rate of related forms from the fossil record.

The growth rate of the branching corals *Thecosmilia* in southern England (text-fig. 4) and *Rhabdophyllia* have been obtained by examination of the epithecal banding. (*T. annularis* is not common in most of the coralliferous localities in Yorkshire and the few specimens collected show only an indistinct banding.) Few measurements were available from Steeple Ashton (though many specimens were examined), but an appreciably lower growth rate is indicated. *R. phillipsi* is not common in the Oxfordian of southern England, and where it occurs, rarely shows well-defined periodic bands. Specimens from a temporary section at Cumnor Hill (SP 465041) show a banding which suggests rates of about 5·0–6·5 mm yr^{-1}. The same range of values is suggested by specimens from Yorkshire localities.
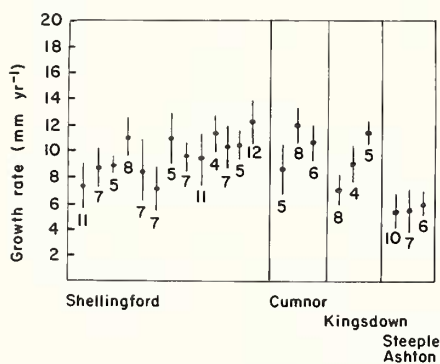

TEXT-FIG. 4. Mean and standard deviation of growth rates of thecosmilian colonies from four localities in the Oxfordian with number of measurements made on each colony.

Growth rates of the massive corals were determined from measurements of the high- and low-density couplets in thin section and cut surfaces. Similar values have been obtained by measurement of epithecal banding. In general there is considerable variation in the thickness of the bands though this is matched by a similar variation in the thickness of individual bands over a colony.

Thamnasteria concinna (text-fig. 5) has the lowest growth rate of the three species but the values show the least variation between colonies and between localities. The growth rate of *Fungiastraea arachnoides* is higher but the variability in the rate is greater. The relatively poor preservation of *Isastraea explanata* has allowed fewer measurements to be made. Values of growth rate vary from 2·5 mm yr^{-1} to about 5·0 mm yr^{-1}. Individual variability in linear growth rate, of much higher magnitude, is reported in modern scleractinians by Lewis *et al.* (1968) for *Acropora* and other corals, and by Weber and White (1974) for *Platygyra*. Weber and White suggest that individual variations in growth rate among the different members of a population are probably attributable to a combination of environmental and genetic factors. Dodge *et al.* (1974) who studied the effect of sediment suspension on growth of *Montastrea annularis* from Jamaica, noted a decrease in the variability of growth with increasing resuspension. They speculated that the ability of the coral to respond to other favourable, or at least less-limiting, environmental variables is reduced by high resuspension. This factor may have applied to the Oxfordian corals under discussion.

TEXT-FIG. 5. Mean growth rates and standard deviation of colonies of *Thamnasteria concinna*, *Fungiastraea arachnoides*, and *Isastraea explanata* from Oxfordian localities with number of measurements made on each colony.
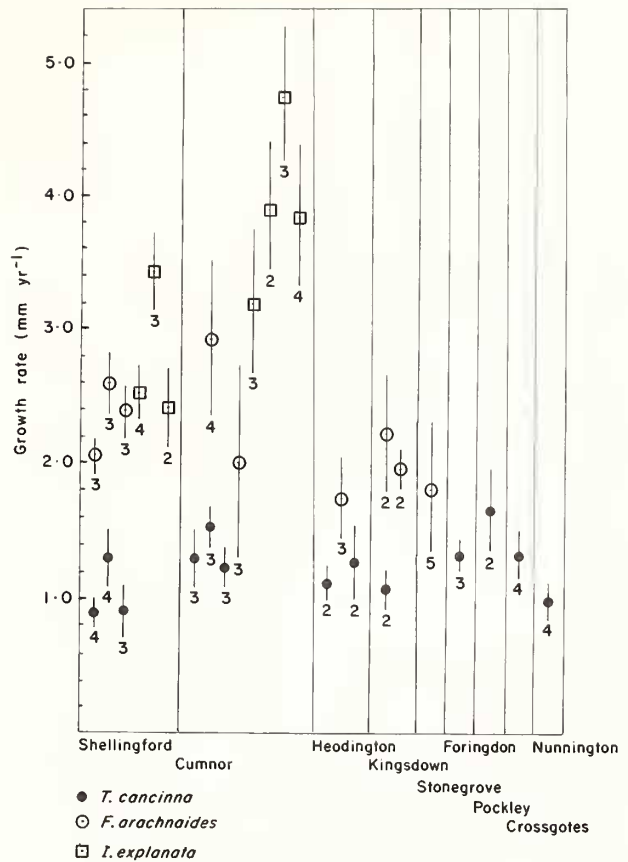
When compared with modern scleractinians the average growth rates of the massive fossil species are low. However, corals such as *Agaracia* (3·5 mm yr⁻¹, Stearn *et al.* 1977), *Solenastrea* (1·5 mm yr⁻¹, Moore and Krishnaswami 1974), and *Siderastrea* (4.1 mm yr⁻¹ Stearn *et al.* 1977) are amongst the slow-growing genera. There are no data available on modern phaceloid genera such as *Caulastrea* and *Astraemorpha*, which are morphologically more similar to *Thecosmilia* and *Rhabdophyllia* than ramose thamnasteroid genera. Vaughan (1915) noted that, in general, the more massive and denser the skeleton the slower the growth, whilst the more ramose and porous the skeleton the more rapid the growth. The growth rates of some Dinantian rugose corals (Johnson and Nudds 1975) are, surprisingly, relatively high (40–60 mm yr⁻¹): though Scrutton and Powell (1981) quote 5–18 mm yr⁻¹ for Silurian favositids.

Extension of growth-rate analysis to estimates of geological time represented by actual sections is fraught with difficulties but two sections were selected in the Oxfordian to attempt to determine the time taken for their formation. Sections at Shellingford Cross-Road Quarry and Ayton Quarry (text-fig. 6) are sufficiently extensive to locate profiles where growth was uninterrupted or where successive generations of coral colonies could be traced. This method was adopted by Hoffmeister and Multer (1964) to estimate growth rate of the Pleistocene Key Largo coral reef of the Florida Keys.

An account of Shellingford Cross-Roads Quarry is being prepared. Arkell (1947, p. 87) gave a general description and Ali (1977) described the effects of penecontemporaneous erosion and mantles of shelly biosparite, and smectite seams which interrupted coral growth. There are three intervals of smectites and three intervals of biosparite but the interruptions ('hazards') to coral growth and
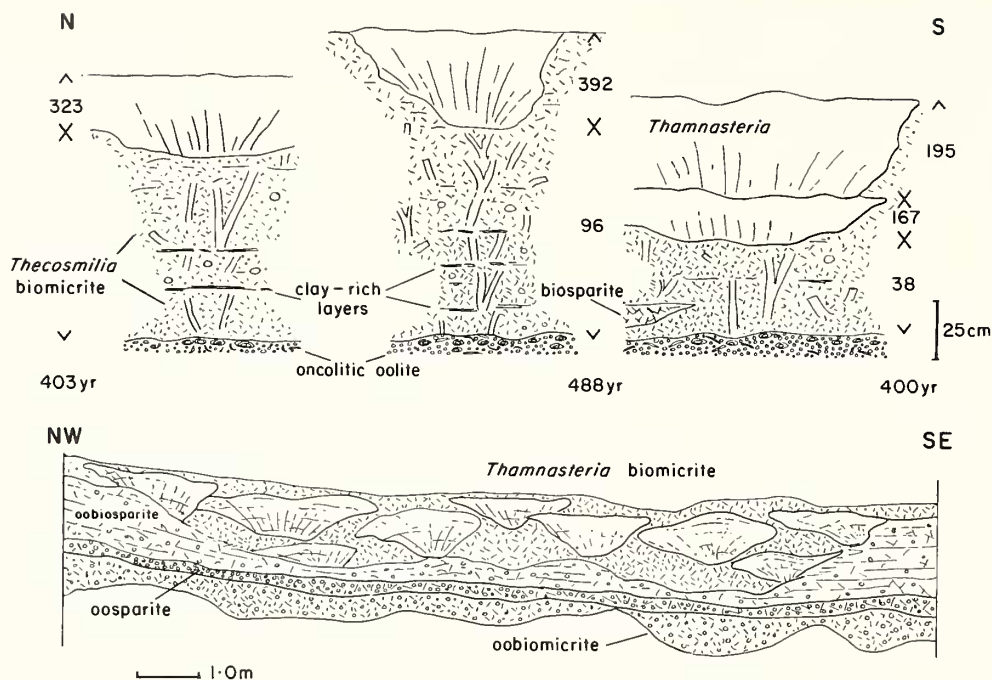
TEXT-FIG. 6. Successive sections used for estimating growth rate of the coralliferous unit at Shellingford Cross-Roads Quarry (above). Sections chosen at about 50-m intervals along quarry face. Lithology and coral distribution at Ayton Quarry (below).

sedimentation were not continuous along the section. When specimens of massive coral are sectioned further local growth discontinuities are evident that are not visible in the field. But such interruptions probably represent only a few years at most. The estimated age for the coralliferous unit is 359 years giving an average growth rate of 3.7 mm yr^{-1}. (This estimate is based on seven sections: data in Ali, unpublished Ph.D. thesis, University of Reading, 1978.)

The section at Ayton Quarry was described and figured by Blake and Hudleston (1877) and referred to by Wright (1972). The coralliferous unit is composed of biolithite with lens-shaped colonies of 1·0 m height forming discrete but closely packed hemisphaeroids averaging 30 cm across, the roundheads of Blake and Hudleston (1877), with little matrix (biomicrite). There are rare colonies of *Rhabdophyllia*. The growth rate of *Fungiastraea arachnoides* forming the column in the centre is about 2·4 mm yr^{-1} and the thickness of this column is about 1·3 m. The minimum period of time required for the formation of the coralliferous unit at Ayton is about 550–600 years.

CARBONATE PRODUCTION

Calcium carbonate production today varies greatly from temperate to tropical environments (Chave *et al.* 1972; Smith 1970, 1971; Stearn *et al.* 1977; Bosence 1980). The data for these studies are based on some assumptions and estimations because of the complexity of the processes within reefs and carbonate banks. As well as the skeletons of the corals and other frame-builders, their epizoans and associated biota, and the sedimentary particles produced by physical and biological erosion and dispersed within and without the reef by currents and waves must also be evaluated.

Chave *et al.* (1972) defined potential production as the amount of calcium carbonate produced by a single organism, or colony of organisms per unit area of the surface covered by that organism. This definition is useful in providing a unit of measurement by which carbonate-producing abilities of different organisms can be compared. With fossil corals the problem is aggravated because not only is it seldom possible to trace time surfaces with any degree of accuracy through a unit, but primary production has been modified subsequently by diagenesis, solution, and precipitation of cements.
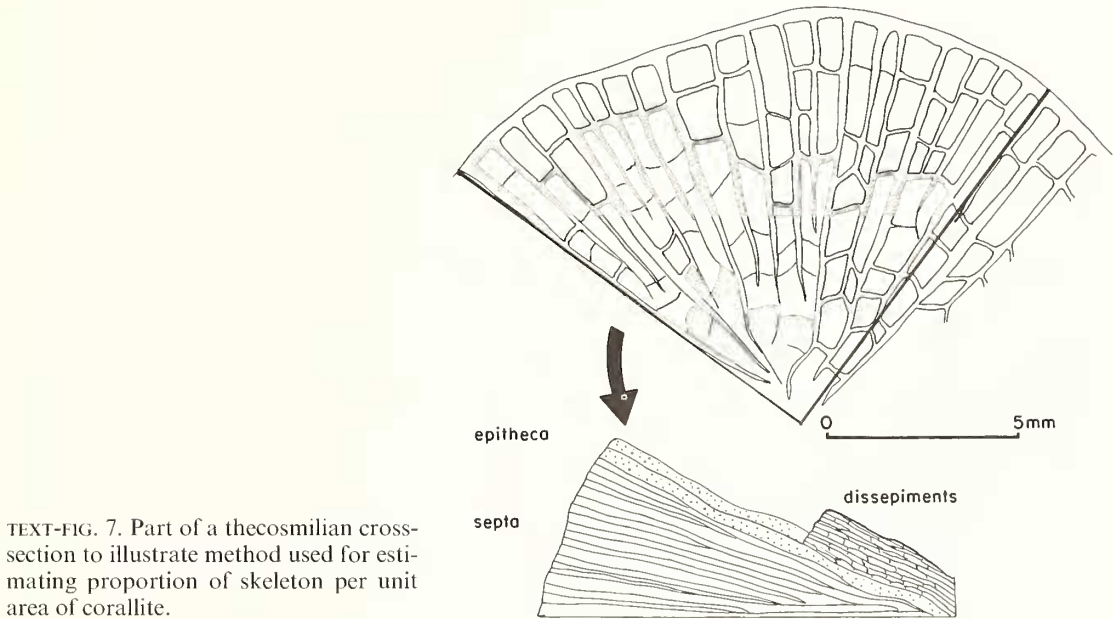
TEXT-FIG. 7. Part of a thecosmilian cross-section to illustrate method used for estimating proportion of skeleton per unit area of corallite.

The method to determine skeletal density of the coral species is shown in text-fig. 7. Successive septa were individually traced, using a low-power projection microscope, on to paper, the paper being moved to give a cumulative value of the septal cross-section areas. Epitheca and dissepiments were then added and the total cross-sectional area determined. It is assumed that *Thecosmilia* had a circular cross-section. The average diameter at Shellingford is about 2·7 cm and aragonite S.G. is 2·94 (Goreau 1963). The skeleton in *Thecosmilia* occupies about 31·5 % of the cross-sectional area. Skeletal proportions of massive corals were determined by the same method and the mass of $CaCO_3$ per unit volume of the organism (g/cm^3) obtained for each species. Potential production, expressed as $CaCO_3$ mass per unit volume × growth rate (cm yr^{-1}) is given in Table 1.

It is clear from the above data that the differences in linear growth rates for the Corallian species are represented by much smaller differences in actual calcification rate because the mass per unit volume of the slower-growing colonies is much higher than in those with faster growth rates.

The estimated values of potential production of massive coral species from Shellingford and from Ayton (Table 1) are quite similar to productivity values of some modern scleractinians off Barbados determined by a different method (Stearn *et al.* 1977), though the calcification rate of *Thecosmilia* is considerably greater.

The gross production is the amount of $CaCO_3$ produced per unit area of the reef (Chave *et al.* 1972). It is obtained by summing the product of potential production of each organism in a given reef, times the proportion of the reef area covered by the organism. The approximate coverage by

TABLE 1. Potential production of coral species and gross production at Shellingford Cross-Roads Quarry and Ayton Quarry

	(a) skeleton per sq. cm	(b) growth rate cm yr^{-1}	(a × 2·94) mass per unit vol. g/cm^3	(a × b × 2·94) potential prodn. g CaCO$_3$ m^2 yr^{-1}	(d) mean coverage^x per unit area	gross prodn. a × b × 2·9 × d
Shellingford, Oxfordshire						
Thecosmilia annularis	0·315	0·98	0·926	9074·8	0·301	2731·5
Thamnasteria concinna	0·588	0·104	1·729	1797·8	0·091	163·6
Fungiastraea arachnoides	0·424	0·235	1·246	2929·4 ⎫	0·128	367·7
Isastraea explanata	0·312	0·28	0·917	2567·6 ⎭		
						3262·8 g CaCO$_3$ m^2 yr^{-1}
Ayton, Yorkshire						
Fungiastraea arachnoides	0·424	0·24	1·246	2990·4	0·4	1196·2
Thamnasteria concinna	0·588	1·04	1·729	2421	0·28	677·8
Rhabdophyllia phillipsi	0·58	0·5	0·90	4500	0·02^y	90·0
						1964·0 g Cal O$_3$ m^2 yr^{-1}

x—based on seven sections (data in Ali, unpublished thesis for Ph.D., University of Reading 1978) *Isastraea* (2%) included with *T. arachnoides*.
y—estimated.

corals at Shellingford is shown in Table 1, together with an estimate of the gross calcium carbonate production of the coralliferous unit. (Where coral cover is extensive gross production on modern reefs is a reasonable approximation of net production: the carbonate permanently retained by the reef after allowance for carbonate dissolution and mechanical gains and losses. In the ancient examples discussed it is appropriate to take net production as equivalent to gross production.)

The coralliferous unit at Ayton is composed mainly of *Thamnasteria* and *Fungiastrea*, but branching *Rhabdophyllia* also occurs forming about 2% of the rock. Estimates of calcium carbonate production for this unit are made by the same method and values are shown in Table 1. Differences in productivity between the two sections are due to small differences in growth rates but mainly to differences in productivity of the species present.

DISCUSSION AND CONCLUSIONS

In upper Jurassic times scleractinians were still at an early stage of their evolution though some, such as the microsolenids (now extinct) had achieved a high degree of integration. Further, Jurassic corals in northwest Europe mostly formed localized banks or patch reefs on an extensive shelf area rather than fringing reefs. Such banks were subdued structures with amplitudes that could mostly be measured in centimetres. During its formation the coralliferous unit at Shellingford Cross-Roads Quarry probably consisted of scattered low domes of massive corals amongst short heads of candle-like thecosmilians and *Rhaxella* sponges emerging from a muddy sediment, with an associated fauna of vagile regular echinoids, brittle stars and small gastropods, and attached oysters and other bivalves as the preservable elements.

Thus it is surprising that this study shows a style of growth banding and values of growth rate and carbonate productivity that compare well with what is known from areas of modern tropical corals, and productivity an order of magnitude higher than temperate coralline algae (Boscnce 1980). Indeed, the values are peculiarly close to the 3–5 kg/CaCO$_3$/m^2 yr^{-1} characteristic of tropical Pacific reef flats (Kinsey 1979, unpublished Ph.D. thesis, University of Hawaii, quoted by Grigg 1982). The possibility that reefs in the Jurassic extended well beyond the 40° latitude to which they are restricted today (Beauvais 1973) cannot be excluded. But the present study is only preliminary and until similar studies have been carried out, particularly on the diverse coral faunas of the northern margin of Tethys, it would be unwise to consider these results as typical for the Mesozoic. The need for more detailed work on modern corals that can be appled to fossil corals is also evident.

REFERENCES

ALI, O. E. 1977. Jurassic hazards to coral growth. *Geol. Mag.* **114**, 63–64.
—— 1983. Microsolenid corals as rock-formers in the Corallian (Upper Jurassic) of England. Ibid. **120**, 375–380.
ARKELL, W. J. 1933. *The Jurassic System in Great Britain.* Clarendon Press, Oxford. Pp. 681.
—— 1947. *The Geology of Oxford.* Clarendon Press, Oxford. Pp. 267.
BAKER, P. A. and WEBER, J. N. 1975. Coral growth rate: variation with depth. *Earth planet. Sci. Lett.* **27**, 57–61.
BARNARD, L. A., MACINTYRE, I. G. and PIERCE, J. W. 1974. Possible environmental index in tropical reef corals. *Nature*, **252**, 219–220.
BEAUVAIS, L. 1973. Upper Jurassic hermatypic corals. *In* HALLAM, A. (ed.) *Atlas of Palaeobiogeography*, 317–328. Elsevier, Amsterdam.
BLAKE, J. F. and HUDLESTON, W. H. 1877. The Corallian rocks of England. *Q. Jl geol. Soc. Lond.* **33**, 260–405.
BOSENCE, D. W. J. 1980. Sedimentary facies, production rates and facies models for recent coralline algal gravels, Co. Galway, Ireland. *Geol. J.* **15**, 91–111.
BUDDEMEIER, R. W. 1974. Environmental controls over annual and lunar monthly cycles in hermatypic coral calcification. *Proc. 2nd int. Symp. on Coral Reefs*, **2**, 259–267. Great Barrier Reef Committee, Brisbane.
—— MARAGOS, J. E. and KNUTSON, D. K. 1974. Radiographic studies of reef coral exoskeletons: rates and patterns of coral growth. *J. exp. mar. Biol. Ecol.* **14**, 179–200.
—— and KINZIE, R. A., III. 1976. Coral growth. *Oceanogr. Mar. Biol. Ann. Rev.* **14**, 183–225.
CHAVE, K. E., SMITH, S. V. and ROY, K. S. 1972. Carbonate production by coral reefs. *Mar. Geol.* **12**, 123–140.
COPE, J. W. C., DUFF, K. L., PARSONS, C. F., TORRENS, H. S., WIMBLEDON, W. A. and WRIGHT, J. K. 1980. A correlation of Jurassic rocks in the British Isles, Part 2, middle and upper Jurassic. *Geol. Soc. Lond. Spec. Paper*, **15**, 109 pp.
DODGE, R. E., ALLER, R. C. and THOMSON, J. 1974. Coral growth related to resuspension of bottom sediments. *Nature*, **247**, 574–577.
—— and THOMSON, J. 1974. The natural radiochemical and growth records in contemporary hermatypic corals from the Atlantic and Caribbean. *Earth Planet. Sci. Lett.* **23**, 313–322.
—— and VAISNYS, J. R. 1977. Coral populations and growth patterns: responses to sedimentation and turbidity associated with dredging. *J. mar. Res.* **35**(4), 715–730.
GOREAU, T. F. 1963. Calcium carbonate deposition by coralline algae and corals in relation to their roles as reef builders. *Ann. N.Y. Acad. Sci.* **109**, 127–163.
GRIGG, R. W. 1982. Darwin Point: a threshold for atoll formation. *Coral Reefs*, **1**, 29–34.
HIGHSMITH, R. C. 1979. Coral growth rates and environmental control of density banding. *J. exp. mar. Biol. Ecol.* **37**, 105–125.
HOFFMEISTER, J. E. and MULTER, H. G. 1964. Growth rate estimates of a Pleistocene coral reef of Florida. *Bull. geol. Soc. Amer.* **75**, 353–358.
HUDSON, J. H. 1981. Growth rates in *Montastraea annularis*: a record of environmental change in Key Largo coral reef marine sanctuary, Florida. *Bull. Mar. Sci.* **31**, 444–459.
—— SHINN, E. A., HALLEY, R. B. and LIDZ, B. 1976. Sclerochronology—a tool for interpreting past environments. *Geology*, **4**, 361–364.

ISDALE, P. 1977. Variation in growth rate of hermatypic corals in a uniform environment. *Proc. 3rd. int. Coral Reef Symp.* 403–408. Rosenthiel School of Marine and Atmospheric Science, Miami.

JEFFERSON, T. H. 1982. Fossil forests from the lower Cretaceous of Alexander Island, Antarctica. *Palaeontology*, **25**, 681–708.

JOHNSON, G. A. L. and NUDDS, J. R. 1975. Carboniferous coral geochronometers. *In* ROSENBERG, G. D. and RUNCORN, S. K. (eds.) *Growth rhythms and the history of the earth's rotation*, 27–41. Wiley, London.

KNUTSON, D. K. and BUDDEMEIER, R. W. 1973. Distribution of radionuclides in reef corals: opportunity for data retrieval and study of effects. *In Radioactive Contamination of the Marine Environment*, 735–746. Vienna International Atomic Energy Agency.

——— ——— SMITH, S. V. 1972. Coral chronometers: seasonal growth bands in reef corals. *Science*, **177**, 270–272.

LEWIS, J. B., AXELSEN, F., GOODBODY, I., PAGE, C. and CHISLETT, G. 1968. Comparative growth rates of some reef corals in the Caribbean. *Marine Science Manuscript report* no. 10. McGill University. Pp. 260.

MA, T. Y. H. 1934. On the seasonal change of growth in a reef coral, *Favia speciosa* (Dana), and the water-temperature of the Japanese Seas during the latest geological times. *Proc. Imp. Acad. Japan (Tokyo)*, **10**, 353–356.

MACINTYRE, I. G. and SMITH, S. V. 1974. X-Radiographic studies of skeletal development in coral colonies. *Proc. 2nd Int. Symp. Coral Reefs*, **2**, 277–287. Great Barrier Reef Committee, Brisbane.

MOORE, W. S. and KRISHNASWAMI, S. 1974. Correlation of x-Radiography revealed banding in corals with radiometric growth rates. *Ibid.* 269–276.

NEGUS, P. E. and BEAUVAIS, L. 1979. The corals of Steeple Ashton (English Upper Oxfordian), Wiltshire. *Proc. geol. Assoc.* **90**, 213–227.

ROSENBERG, G. D. and RUNCORN, S. K. (eds.) 1975. *Growth rhythms and the history of the Earth's Rotation*. Wiley. Pp. xvi + 559.

SCRUTTON, C. T. 1978. Periodic growth features in fossil organisms and the length of the day and month. *In* BROSCHE, P. and SÜNDERMANN, J. (eds.) *Tidal Friction and the Earth's Rotation*, 154–196. Springer.

——— POWELL, J. H. 1980. Periodic development of dimetrism in some favositid corals. *Acta Palaeont. Polonica.* **25**, 477–491.

SMITH, A. G., HURLEY, A. M. and BRIDEN, J. C. 1981. *Phanerozoic palaeocontinental world maps*. Cambridge University Press. Pp. 1620.

SMITH, S. V. 1970. Calcium carbonate budget of southern Californian Borderland, *Hawaii Inst. Geoph. Rpt.*, HIG 70–11, 174 pp.

——— 1971. Budget of calcium carbonate, Southern California continental Borderland. *J. sedim. Petrol.* **41**, 798–808.

STEARN, C. W., SCOFFIN, T. P. and MARTINDALE, W. 1977. Calcium carbonate budget of a fringing reef on the west coast of Barbados. 1. Zonation and productivity. *Bull. mar. Sci.* **27**, 479–510.

VAUGHAN, T. W. 1915. The geologic significance of the growth rate of the Floridian and Bahaman shoal-water corals. *J. Wash. Acad. Sci.* **5**, 591–600.

WEBER, J. N. and WHITE, E. W. 1974. Activation energy for skeletal aragonite deposited by the hermatypic scleractinian coral *Platygyra* spp. *Mar. Biol.* **26**, 253–259.

——— ——— WEBER, P. H. 1975. Correlation of density banding in reef coral skeletons with environmental parameters: the basis for interpretation of chronological records preserved in the coralla of corals. *Paleobiology*, **1**, 137–149.

WRIGHT, J. K. 1972. The stratigraphy of the Yorkshire Corallian. *Proc. Yorks Geol. Soc.* **39**, 225–266.

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